

THE SPECIES *BUFO GRANULOSUS* SPIX (SALIENTIA: BUFONIDAE) AND ITS GEOGRAPHIC VARIATION

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INTRODUCTION

The present paper is part of a general study of the neotropical Bufonidae. In an earlier paper (1957) I discussed *Bufo granulosus* Spix and its distribution in Argentina; I now consider it in its entire range. Through the kindness of the authorities of several North and South American and European museums, I have examined 813 specimens; those studied in my earlier work bring the total to 1,198 specimens. I have thus been able to see a large proportion of the specimens cited in the literature, including types, paratypes, and topotypes. The materials studied belong to the following institutions, listed in order of abbreviation: American Museum of Natural History, New York (AMNH); The Academy of Natural Sciences of Philadelphia (ANSP); British Museum (Natural History), London (BMNH); Carnegie Museum, Pittsburgh (CM); Chicago Natural History Museum (CNHM); Instituto e Museo di Zoologia della Università di Torino (IMZUT); Institut Royal des Sciences Naturelles de Belgique, Brussels (IRSN); Museo Argentino de Ciencias Naturales, Buenos Aires (MACN); Museo Civico di Storia Naturale "G. Doria," Genoa (MCSN); Museum of Comparative Zoology, Cambridge (MCZ); Muséum National d'Histoire Naturelle, Paris (MNHN); Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); Museum of Zoology of the University of Michigan, Ann Arbor (MZUM); Rijksmu-

seum van Natuurlijke Historie, Leiden (RNH); Senckenberg Museum, Frankfurt (SM); Facultad de Ciencias, Universidad Central de Venezuela, Caracas (UCV); United States National Museum, Washington (USNM); Zootomiska Institutet (University of Stockholm) (ZIUS); Zoologische Museum Berlin (ZMB); Zoologische Sammlung des bayerischen Staates, Munich (ZSBS). The gathering together and examination of these very large collections at the Museum of Comparative Zoology—at one time and in one place—has enabled me to reach new decisions.

HISTORICAL SUMMARY

The history of the classification of this species can be summarized as follows:

Spix (1824: 49, pl. 19, fig. 1, and 51, pl. 21, fig. 2) described the species under two different names, *Bufo globulosus* and *Bufo granulosus* (basing both names on specimens from the state of Bahia, Brasil). The vicissitudes of these two names and final prevalence of the second over the first may be followed in my earlier work on the species (Gallardo, 1957: 338–340).

Seventeen years later, Duméril and Bibron (1841: 697–698) described a toad from Uruguay under the name *Bufo dorbignyi*. When specimens from northern Brasil are compared with this one from Uruguay they prove to be quite different, especially with regard to the cephalic crests, low in the former and enormous in the latter. For this reason the two forms were considered

different species for many years. However, as more material has brought increase in knowledge of the amphibians of South America, *Bufo granulosus* and *B. dorbignyi* were cited randomly from localities between the type localities of the two taxa. Parker (1935: 509), studying specimens of *B. granulosus* from British Guiana, considered it probable that *B. dorbignyi* was only a subspecies of *B. granulosus*, since, according to him, the two intergraded in the Asunción region (Paraguay). Following this idea, Müller and Hellmich (1936: 7-14, fig. 3) recognized three subspecies of *B. granulosus*: *B. g. granulosus*, *B. g. major* and *B. g. dorbignyi*. Subsequently, most authors have considered *B. dorbignyi* as a subspecies of *B. granulosus*. Other authors reported differences, possibly of subspecific rank, between specimens of *B. granulosus* from different localities. Thus, Schmidt and Inger (1951: 444) observed that specimens from the state of Amazonas in Brasil have smooth crests, while those from Ceará, Paraíba, and Rio Grande do Norte have denticulate crests. Myers and Carvalho (1952: 1) considered it probable that several subspecies of *B. granulosus* may be differentiated. They cited differences between some localities in Brasil: for example, specimens from Araguaia (Rio Tapirapé) have a "flattened muzzle," differing from others from Pirapora (Minas Gerais), while a third type was found in Manáos and Santarém. Similarly, examples from São Luiz de Cáceres with "shortened physiognomy and strong infranarial crest," are close to others from Asunción (Paraguay). Myers and Carvalho have also described a species from the state of Rio de Janeiro, *Bufo pygmaeus*, which they considered close to *B. granulosus*.

In my earlier work (1957) I recognized three forms in Argentina: *B. g. dorbignyi*, *B. g. fernandezae* and *B. g. major*. After studying much more material, I have changed my concept of the typical subspecies *B. g. granulosus* (1957: 366-368) which I supposed would reach northern Paraguay;

actually what occurs in this region is *B. g. major*, while *B. g. mirandaribeiroi* subsp. nov. occurs in central Brasil, *B. g. granulosus* being restricted to northeastern Brasil.

As I stated for the Pseudidae (Gallardo, 1961), one can see in *B. granulosus* a clear distribution of the subspecies according to the hydrographical systems, a distinct subspecies belonging to the basin of each of the following rivers: Magdalena, Orinoco, Upper and Middle Amazon, Tocantins and Araguaia, São Francisco, Rio de la Plata. Because of this there are on occasion at nearly the same geographical latitude and a few kilometers apart two or three different subspecies, corresponding to different hydrographical systems; this occurs, for example, in Mato Grosso. Other subspecies belong to zones between basins or at the edge of the large basins; thus, distinct subspecies occur in a part of Uruguay and in southern Brasil, in the Chaco, in northwestern Bolivia, in northeastern Brasil, and in the Guianas. Some islands, such as Margarita Island near the Venezuelan coast, have their own subspecies; in others, such as Trinidad, the same subspecies exists as in the Orinoco basin.

SYSTEMATIC DESCRIPTIONS

Bufo granulosus Spix

Description of the species as a whole. Nostrils prominent. Supraorbital, preorbital, postorbital, suborbital, orbitotympanic, parietal, subnasal, canthal, and maxillary cephalic crests more or less well developed (in some subspecies very little developed and sometimes one or more absent); the crests may be granular, rippled or with smooth border according to the subspecies. The maxillary crest is smooth-bordered in all subspecies. The width of the interorbital space varies directly with the development of the supraorbital crest. Tympanum elliptic with the larger diameter dorsoventral, two-thirds the larger diameter of the eye. In some subspecies the tympanum is not very evident. First finger shorter than the second; subarticular tubercles double, especially evident on second

and third fingers; edge of fingers granulate, except the distal extreme. Palms with granulations usually conical, sometimes rounded; outer metacarpal tubercle large and irregularly round, inner tubercle small and elliptic. Hind limbs short, the tibio-tarsal articulation reaching shoulder or tympanum. First and second toes very short; double subarticular tubercles on the fourth toe; interdigital membrane reaching the toe tips, except in the fourth toe where it is present only at the base but is prolonged as a serrated cutaneous fringe to the tip; outer metatarsal tubercle not so prominent as the innermost, both conical, oblique. No tarsal fold, sometimes a line of spinous granules. Parotoids in general not very prominent, with lower edge not very evident; their lateral granules conical, the dorsal ones conical or rounded according to the subspecies. Granulations of the dorsum varying in shape in the subspecies, but in general the anterior are rounded, the lateral and posterior ones conical. Conical granulations on the limbs. Ventral skin with granules, smaller and abundant anteriorly, larger and sparser posteriorly.

Dorsum yellowish or greenish, with large dark spots. A vertebral light line exists in some subspecies but is absent in others. Belly yellowish.

Secondary sexual characters: males with one subgular medial vocal sac and darker skin in this region; first and second fingers dorsally brown (sometimes also the inner metacarpal tubercle). Females larger and with gular and pectoral granulations with small horny points.

Characters for the differentiation of the subspecies. In distinguishing the subspecies of *B. granulatus*, I found the following characters especially useful: the shape of the head; the degree of obliquity of the loreal region; the development of the snout; the shape of the rostrum, vertical or oblique; the position of the nostrils; the development of the cephalic crests, the characteristics of each crest, especially the maxillary and suborbital crests; the width, depth and



Map 1. Approximate ranges of the subspecies of *Bufo granulatus*: 1. *B. g. humboldti*; 2. *B. g. barbouri*; 3. *B. g. beebei*; 4. *B. g. merianae*; 5. *B. g. goeldii*; 6. *B. g. minar*; 7. *B. g. mirandaribeirai*; 8. *B. g. lutzi*; 9. *B. g. granulatus*; 10. *B. g. major*; 11. *B. g. azorai*; 12. *B. g. fernandezae*; 13. *B. g. pygmaeus*; 14. *B. g. dorbignyi*.

granulations of the interorbital space; tympanum more or less evident, the plane of slope of the tympanum; the prominence of the parotoids and the type of their dorsal granulations; the presence or absence of a row of granules on the inner tarsal edge; and the presence or absence of the vertebral line. For certain determination of the subspecies it is necessary to take into consideration all these characteristics.

Distribution of the species. *Bufo granulatus* extends from Rio Calobre in Panama, to the Sierra de la Ventana, Buenos Aires Province, Argentina. It occurs in Colombia, Venezuela, Margarita and Trinidad islands, British and Dutch Guianas, Brasil (in all of its territory), northeast Peru, non-Andean Bolivia, Paraguay, Uruguay and Argentina

(Chacoan region, Mesopotamia, Santa Fé and Buenos Aires Province). Noticeable in this distribution is its absence in western South America; it has never been reported from Ecuador (though perhaps it exists in the Amazonian eastern part of that country), nor in most of Peru, in western Bolivia, in Chile, nor in western and southern Argentina. It does not extend as far to the west as *B. typhlonius*, which has a wider distribution from Panama to Bolivia and from the Guianas and Brasil to Ecuador and Peru. In Argentina (Gallardo, 1957: 337), *B. granulatus* does not extend as far west and south as *B. arcuatum*, which is a species very closely related to *B. rufus* of Minas Gerais (Brasil) and to *B. poeppigii* of eastern Peru.

***Bufo granulatus granulatus* Spix**

Bufo granulatus Spix, 1824, p. 51, pl. 21, fig. 2 (type locality, Bahia); Martius, 1840, p. 27, pl. 21, fig. 2; Günther, 1858, p. 67 (part), pl. V, fig. A; Peters, 1873, p. 225; Boulenger, 1882, p. 324 (part); de Witte, 1930, p. 229; Schubart, 1939, p. 56; Schmidt and Inger, 1951, p. 444 (part).

Bufo globulosus Spix, 1824, p. 46, pl. 19, fig. 1 (type locality, Rio Itapicuru); Martius, 1840, p. 25, pl. 19, fig. 1; Peters, 1873, p. 223; Lutz, 1934, p. 124 (part), est. XXVII, fig. 6; Miranda Ribeiro, 1937, p. 56; Carvalho, 1937, p. 12.

Description. Adult male, USNM 97107, state of Bahia, Brasil. Head short, wide and high; loreal region nearly vertical. Snout short, though in ventral view the muzzle appears to project. Rostrum nearly vertical, but slightly sloping. Nostrils elongate, in some oblique. Cephalic crests low, with granular or scalloped border, except the maxillary crests which have smooth borders. Subnasals scarcely visible. Cantilals visible, with granular borders. Suborbitals very near the lower edge of eye, not prolonged beyond the postorbitals. Preorbital crests well defined. Postorbital crests well defined, close to the anterior border of the tympanum and sloping anteriorly. Maxillary crests not expanded laterally; when the head is viewed dorsally, they are hidden by the suborbitals, and in ventral view there is not

a conspicuous maxillary rim. Supraorbital crests low, the interorbital space slightly concave and granular. Parietal crests scarcely or not marked. Orbitotympanic crests present, but not well marked. Tympanum distinct, sloping outward. Parotoids not prominent, 9.5 mm long, with rounded dorsal granulations. One row of spinous granules on the tarsal internal edge.

Dorsal coloration. Orange with a black reticulum, interscapular space generally lighter but without well-defined vertebral light line (only a longitudinal medial groove). Belly yellowish.

Dimensions (in mm). Head and body 55. Head length 13. Head width 18. Head height 7. Eye 5. Interorbital space 6. Upper eyelid width 4. Elbow to third finger 23. Femur 19. Tibia length 19. Tibia width 6. Heel to fourth toe 28. Foot 12. Female, USNM 97109, same locality, head and body 56 mm.

Variation. In large animals the crests are continuous and with irregular borders. Cantil crests may be absent (a specimen from Baixa Verde, Rio Grande do Norte). Parietal crests present or absent. Subarticular tubercles of hand and foot sometimes simple.

Distribution. This form was described by Spix (1824) from the Rio Itapicuru and Bahia (state of Bahia, Brasil); its range is northeast Brasil: Itaeté, Joazeiro, Bonfim (Bahia), Tapera, Bonito (Pernambuco), Independencia (Paraíba), Natal, Ceará Mirim, Baixa Verde (Rio Grande do Norte).

Remarks. The types of *B. globulosus* and *B. granulatus* in the Zoologische Sammlung des bayerischen Staates in Munich were destroyed during World War II, according to a letter from Dr. W. Hellmich.

Literature citations referred to this subspecies. Günther (1858: 67), Pernambuco; Boulenger (1882: 324), Pernambuco only [I have seen BMNH 1881-7.4.8, Forbes coll.]; de Witte (1930: 229), Itaeté, Bahia [IRSN 71, examined]; Lutz (1934: 124), only Natal, Rio Grande do Norte; Schubart (1939: 56), localities in Pernambuco;

Schmidt and Inger (1951: 444), specimens from Paraíba and Rio Grande do Norte, probably also those from Ceará [material examined: CNHM 64198–210]; Cochran (1955: 24–25), specimens from Bahia, Pernambuco, Rio Grande do Norte, probably also those from Ceará [some of these specimens examined].

The specimens reported as *Bufo globulosus* by Miranda Ribeiro (1937: 56) and Carvalho (1937: 12) also belong to the present subspecies.

Material studied. **Brasil.** *Bahia.* Itaeté, IRSN 71 (3 specimens). Bonfim, CM 2650. Joazeiro, MZUM 108914 (1 specimen), USNM 98839. Estado de Bahia, USNM 97107–9. *Pernambuco.* Tapera, MCZ 15368. Bonito, MCZ 2059. Pernambuco, CNHM 42204, BMNH 1881 7.4.8, USNM 57877. Estado Pernambuco, MCZ 1502. *Paraíba.* Independência, CNHM 64198–9. *Rio Grande do Norte.* Natal, USNM 81140, MZUM 74326. Ceará Mirim, CNHM 64201–10. Baixa Verde, CNHM 64200.

***Bufo granulosus goeldii* subsp. nov.**

Bufo granulosus Cope, 1874, p. 120; Schmidt and Inger, 1951, p. 444 (part); Myers and Carvalho, 1952, p. 1 (part).

Holotype. MZUM 64528, adult male, Santarém, Pará, Brasil.

Paratypes. MZUM 122431–34, 4 males, same data; MCZ 353, female, also Santarém.

Description of type. Head short, wide and high; loreal region nearly vertical. Snout very short, but prominent. Rostrum nearly vertical. Nostrils elongate and oblique. Cephalic crests medium in development, generally with borders between smooth and rippled. Canthal crests with smooth borders. Subnasal crests distinct and with smooth borders. Suborbital crests little separated from the lower margin of the eye, some laterally expanded and not reaching beyond the postorbitals. Preorbitals oblique from front to rear. Postorbital crests near the anterior tympanic border and sloping forward. Maxillary crests with smooth borders, somewhat expanded laterally; in dorsal view the maxillary crests projecting

somewhat laterally; in ventral view they are seen as a distinct rim. Supraorbital crests not very high, interorbital space not very wide, with but little concavity and with short divergent crests at the canthal apex, medially smoother, posteriorly with small granules. Parietal crests marked. Orbitotympanic crests present and well marked. Tympanum sloping outward. Parotoids not prominent, length 8 mm, dorsal granules rounded. Granulations on dorsum few and small. One row of spinous granules on the inner tarsal edge. No vertebral light line, instead long oblique light and dark spots. Belly light yellowish.

Dimensions of type (in mm). Head and body 55. Head length 14. Head width 19. Head height 8. Eye 6. Interorbital space 7. Upper eyelid width 4. Elbow to third finger 23. Femur 21. Tibia length 19. Tibia width 6. Heel to fourth toe 29. Foot 19. Female paratype, MCZ 353, head and body 65 mm.

Variations. Sometimes no parietal crests or canthal crests, or suborbital crests not well marked. At the boundary of the subspecies area there are some forms transitional to other subspecies. Thus the Villa Murtinho specimens show a tendency towards *B. g. major*. In some specimens there is a partial vertebral line anteriorly. In juveniles the cephalic crests are more granular. Size range: males 40.5–55 mm; females 46.5–65 mm.

Distribution. *B. g. goeldii* extends over a large part of the Amazonas basin, from Santarém to the Upper Amazonas. It is known in Brasil from Santarém, Tapajóz, Obidos (state of Pará), Manáos, Lago Aleixo, Itacoatiara, Boa Hora (state of Amazonas), Villa Murtinho, Pôrto Velho (Guaporé Territory), and in Peru from the Rio Marañón. To the Southwest it meets *B. g. minor* and *B. g. major*.

Remarks. I name this subspecies in honor of Dr. E. A. Goeldi, student of the Amazonas fauna.

Literature citations referred to this subspecies. Cope (1874: 120), Rio Marañón,

Peru [material examined ANSP 14257, MCZ 4773]; Schmidt and Inger (1951: 444), Itacoatiara, state of Amazonas [material examined: CNHM 64184-97, 64211-14]; Myers and Carvalho (1952: 1), Manáos, Santarém; Cochran (1955: 24), Pôrto Velho [material examined: MZUM 56777].

Material studied. **Brasil.** Amazonas. Santarém, MZUM 64528 (5 specimens), BMNH 1896.6.29.7-11, MCZ 353 (2 specimens), MCZ 400. Tapajóz, ANSP 25229, MCZ 1627 (5 specimens). Obidos, Rio Trombetas, MZUM 80402, MZUM 48295. Itacoatiara, CNHM 64184-97, 64211-14. Manáos, MCZ 1257. Bôa Hora, MZUM 57600. Pôrto Velho, MZUM 56763, 56768-9, MZUM 56773, 56777, 56778 (10 specimens). Villa Murtinho, MZUM 56764-67, 76078. Lago Aleixo, MCZ 17670. **Peru.** "Peru," ANSP 14257, MCZ 4773.

***Bufo granulosus merianae* subsp. nov.**

Bufo granulosus Günther, 1858, p. 142; Boulenger, 1882, p. 324 (part); Van Lidth de Jeude, 1904, p. 93; Tate, 1932, p. 244.

Bufo globulosus Parker, 1935, p. 509.

Bufo strumosus Duméril and Bibron, 1841, p. 716 (part).

Holotype. AMNH 46531, adult male, head falls of Essequibo River, British Guiana.

Paratypes. AMNH 46525-30 + 10 specimens, same data.

Description of type. Head short, expanded laterally, high; loreal region nearly vertical. Snout short, but prominent. Rostrum nearly vertical. Nostrils elongate and somewhat oblique. Cephalic crests projecting, generally with rippled borders. Canthal crests marked, with smooth borders. Subnasal crests visible. Suborbital crests with little separation from the lower border of the eye, prolonged beyond the postorbital crests. Preorbital and postorbital crests together with the supraorbitals make a projecting rim around the eyes; the preorbitals slope to the rear; postorbitals near the anterior border of the tympanum. Maxillary crests with smooth borders, somewhat expanded in dorsal view; suborbital crests

projecting laterally; in ventral view the maxillary crests appear as a rim. Supraorbital crests projecting and rippled, with short oblique crests in the interorbital space; interorbital space concave, and granular, with the short divergent crests of the canthal apex hardly visible. Parietal crests scarcely marked. Orbitotympanic crests marked. Tympanum nearly vertical. Parotoids large, but not very prominent, length 10 mm; dorsal granulations rounded. One row of spinous granules on the inner tarsal edge. No vertebral light line; general coloration yellowish with long black spots. Ventral region gray-yellowish with dark spots.

Dimensions of type (in mm). Head and body 54. Head length 14. Head width 19. Head height 8. Eye 6. Interorbital space 9. Upper eyelid width 4. Elbow to third finger 24. Femur 17. Tibia length 17. Tibia width 7. Heel to fourth toe 28. Foot 19. Female paratype, AMNH 46525, head and body 70 mm.

Variations. Sometimes the parietal crests are well marked. The postorbital crests are far from anterior border of tympanum, especially in small animals. The vertebral light line is sometimes scarcely marked, in others distinctly visible. Sometimes there is a characteristic dorsal dark pattern: a reverse V between shoulders, a sacral rectangle, a supraclacal M and a circle upon each thigh. Ventrally, wholly light or with some dark spots. The specimens from near Mount Roraima show some differences: large and prominent reddish parotoids; wide dorsal black bands; ventrally many dark spots forming a reticulum. Size range: males 32.5-59.5 mm; females 36-72 mm.

Juvenile characters. Cephalic crests granular. Dorsum gray with well-defined darker spots; interocular, three spots between shoulders, one latero-abdominal and a supraclacal triangle; limbs striped. Belly spotted.

Distribution. British Guiana (head falls of Essequibo River, Rupunumi River and Savannah, Isheartum, Wismar) and Surinam

(King Frederick William Falls, Saramacca, Zanderij). It also occurs in the adjacent region of Brasil (Paulo near Mount Roraima, Pacaraima, San José, Roraima) and Venezuela (Arabupu, Santa Elena, Cuquenán).

Remarks. I name this subspecies in honor of Marie Sybille Merian for her work on the Surinam fauna (1771).

Literature citations referred to this subspecies. Duméril and Bibron (1841: 718), Guiana, Cayenne ("*Bufo strumosus*"); Günther (1858: 142), Surinam; Boulenger (1882: 324), Surinam [material examined: BMNH 1858.11.25.153]; Van Lidth de Jeude (1904: 93), Lower Nickeri, Surinam [probable; not seen]; Parker (1935: 509), Rupununi, Savannah and Pacaraima foothills, British Guiana ("*Bufo globulosus*") [material examined: BMNH 1933.6.19.33–35; the marked development of the crests in this subspecies resembles that of *B. g. fernandezae* and *B. g. dorbignyi* and this character probably influenced Parker to suggest that *B. dorbignyi* was a subspecies of *granulosus*]; Cochran (1955: 25), Mount Roraima ("*B. g. granulatus*").

Material studied. **Brasil.** San José, AMNH 49383–4. Mt. Roraima, AMNH 3750. **British Guiana.** Paulo, Mt. Roraima, AMNH 39739–50, 39754, 39760. Pacaraima foothills, BMNH 1933.6.19.35. Head falls of Essequibo River, AMNH 46525–31. Rupununi River, AMNH 46484–93 (29 specimens). Upper Rupununi River, AMNH 46446–50. Rupununi Savannah, BMNH 1933.6.19.33–4. Wismar, AMNH 45761. Isheartun, AMNH 44544. King Frederick William Falls, BMNH 1936.9.3.19–20. **Surinam.** King Frederick William Falls, CNHM 30911. Near Saramacca River, kilometer 91.5, BMNH 1946.4.1.82–89. Zanderij, BMNH 1946.4.2.88, 92, 98, BMNH 1946.4.2.1–3 and 1946.4.1.90–91, 93–97. "Surinam," ANSP 2632–3. "Dutch Guiana," BMNH 1858.11.25.153. **Venezuela.** Arabupu, MZUM 85132–35 (13 specimens). Santa Elena, MZUM 85131. Seven miles from Cuquenán, MZUM 85130.

Bufo granulatus minor subsp. nov.

Bufo granulatus Boulenger, 1898a, p. 5.

Holotype. MCZ 10089, adult male, Upper Beni below mouth of Mapiri, Bolivia.

Paratypes. MCZ 10090, same data; MZUM 57592 (15 specimens), same locality.

Description of type. Head short, wide and high; loreal region somewhat concave. Snout short, but prominent. Rostrum nearly vertical. Nostrils elongate, somewhat oblique. Cephalic crests somewhat projecting, generally with rippled borders. Canthal crests with smooth borders. Subnasal crests present and projecting. Suborbital crests close to the lower margin of the eye, not reaching beyond the postorbitals. Preorbitals and postorbital crests somewhat projecting; postorbital crests close to the tympanum. Maxillary crests with smooth borders, somewhat expanded; in dorsal view the maxillary crests project laterally; ventrally the maxillary crests appear as a rim. Supraorbital crests slightly projecting, interorbital space concave, with small divergent crests in the canthal apex and with granules in the parietal region. Parietal crests marked. Orbitotympanic crests marked. Tympanum nearly vertical. Parotoids prominent, but with lateral border not well marked, length 8 mm; dorsal granules rounded and horny. A row of spinous granules on the inner tarsal edge.

No vertebral light line. Dorsum brown, with light interorbital space and with a light triangle between shoulders and sacral region. Belly light.

Dimensions of type (in mm). Head and body 50. Head length 12. Head width 16. Head height 6. Eye 5. Interorbital space 6. Upper eyelid width 3. Elbow to third finger 22. Femur 15. Tibia length 13. Tibia width 6. Heel to fourth toe 26. Foot 17. Female paratype, MZUM 57592, head and body 51 mm, same locality as type. Size range: males 36–50 mm; females 39.5–51 mm.

Distribution. *B. g. minor* occurs in northern Bolivia in the Upper Beni River region:

Reyes, Rurrenabaque, Cachuela Esperanza and Muyurina, below the mouth of the Mapiri River. It adjoins *B. g. major*, with which it has some characteristics in common.

Remarks. The name of this subspecies is given on account of its small size, contrasting with *B. g. major*, geographically close but of large size in general, as indicated by the name.

Literature citations referred to this subspecies. Boulenger (1898a: 5), various localities in Bolivia, i.e., Reyes, Santa Ana de Marinos, Misiones Mositenes. [I have seen specimens only from the first locality (MCSN 29800) but probably those from the other localities mentioned belong to this subspecies.]

Material studied. **Bolivia.** Santa Cruz, Muyurina, USNM 142103-4; Upper Beni, below mouth of Rio Mapiri, MZUM 57588, 57592, 57595 (21 specimens), MCZ 10089-90; Reyes, right bank of Beni River, MCSN 29800 (2 specimens); Rurrenabaque, MZUM 57587, 57589, 57594 (12 specimens); Cachuela Esperanza, MZUM 57593 (5 specimens).

***Bufo granulosus beebei* subsp. nov.**

Bufo granulosus Ruthven, 1922, p. 55 (part); Lutz, 1928, p. 89, est. 16, figs. 5-6; Parker, 1933, p. 11; 1936, p. 1; Beebe, 1952, p. 174; Lynn, 1959, p. 113.

Bufo globulosus Lutz, 1927, p. 42, est. 8, figs. 5-6; 1934, p. 124 (part), est. XXV.

Holotype. AMNH 55774, adult male, Churchill-Roosevelt Hwy., Trinidad, B.W.I.

Paratypes. AMNH 55771, 55773, 55775 + 8 duplicate specimens, same data.

Description of type. Head elongate, not wide, depressed; general body shape pyriform. Loreal region oblique. Snout elongate. Rostrum sloping. Nostrils elongate and oblique. Cephalic crests not very prominent with smooth or somewhat rippled borders. Canthal crests with smooth borders. Subnasal crests indistinct. Suborbital crests close to the lower border of the eye, continued just beyond the postorbitals by granules. Preorbital crests projecting, forming a small flange in front of the eyes, sloping to

the rear. Postorbital crests close to the anterior border of the tympanum and sloping in front. Maxillary crests with smooth borders, scarcely expanded; in dorsal view the suborbitals project somewhat laterally; ventrally, the maxillary crests appear as a narrow rim. Supraorbital crests but little raised, with short divergent crests on the parietal region; interorbital space somewhat concave, with granules and small divergent crests in the canthal apex. Parietal crests visible, but very short. Orbitotympanic crests well marked. Tympanum slightly sloping outward. Parotoids large, length 8.5 mm; dorsal granules large, rounded and flat. One row of spinous granules on the inner tarsal edge.

Vertebral light line absent or just visible anteriorly. General color light brown, with two reversed dark V's on the dorsal medial line, the more anterior one forming an "X" with the parietal crests. Limbs transversely striped. Belly light, with indistinct dark spots.

Dimensions of type (in mm). Head and body 43. Head length 11. Head width 15. Head height 5. Eye 4. Interorbital space 6. Upper eyelid width 3. Elbow to third finger 19. Femur 14. Tibia length 15. Tibia width 5. Heel to fourth toe 23. Foot 15. Female paratype, AMNH 55771, head and body 48 mm.

Variation. There is one specimen transitional to *B. g. humboldti*, with short snout, from Sucre, Venezuela. (It is on the basis of this specimen that I regard *beebei* as a subspecies of *B. granulosus*.) In some specimens there is a very slender vertebral line; in others it is partly or wholly absent. The ventral region may be light or with small dark spots. Size range: generally of small size, males 35.5-51 mm, females 47-53 mm.

Distribution. Along the Rio Orinoco basin, in Venezuela (San Fernando de Atabapo, Upper Orinoco, Puerto Ayacucho, Maracay, Uruyen); it occurs also in Falcon and Sucre states (Cumanacoa). It is also recorded by specimens from Gaira (Colom-

bia), and Trinidad (San Rafael, St. Augustine, Churchill-Roosevelt Hwy.).

Remarks. I name this subspecies after Dr. William Beebe, explorer of Trinidad.

Literature citations referred to this subspecies. Lutz (1927: 42, pl. 8, figs. 5–6; 1928: 89, pl. 16, figs. 5–6; 1934: 124, pl. 25), Maracay, Venezuela [I have seen USNM 97193–5]; Cochran (1955: 25); Parker (1933: 11), Trinidad; Beebe (1952: 174), Arima Valley, Trinidad; Lynn (1959: 113), St. Augustine, Trinidad; Parker (1936: 1), Upper Orinoco, Venezuela [material examined: IRSN 71].

Material studied. **Venezuela.** *Terr. Fed. Amazonas.* Upper Orinoco, IRSN 71 (2 specimens), UCV 13, 28–29, 41–47. San Fernando de Atabapo, MCZ 27825. Puerto Ayacucho, Rio Orinoco, AMNH 23220–1. *Bolivar.* Urogen, UVC 3166. *Aragua.* Maracay, USNM 97193–5. *Sucre.* Cumanacoa, CM 9028, 9054, 9096. *Falcon* ? “Venezuela,” UCV (15 specimens). **Colombia.** Gaira, MZUM 45527. **Trinidad.** “Trinidad,” CNHM 43667. St. Augustine, MCZ 19889 (2 specimens). San Rafael, CNHM 49603–4. Churchill-Roosevelt Hwy., AMNH 55770–78 (29 specimens).

Bufo granulosis barbouri subsp. nov.

Bufo granulosis Brongersma, 1948, p. 90, fig. 30.

Holotype. RNH 10867, adult male, Porlamar, Isla Margarita, V-25-1936.

Paratypes. RNH 10868, same data, 1 female and 9 males.

Description of type. Head moderately elongate, somewhat wide, depressed; body wide. Loreal region slightly sloping, with small broken crests. Snout prominent, short and wide. Rostrum somewhat sloping. Nostrils elongate and oblique. Cephalic crests somewhat elevated and in general with lightly rippled borders. Canthal crests with smooth borders. Subnasal crests visible. Suborbital crests near lower border of the eye, reaching a little beyond the post-orbitals. Preorbital crests not very salient, sloping posteriorly. Postorbital crests separated from the tympanum. Maxillary crests

with smooth borders, but little expanded; in dorsal view, the suborbital crests projecting laterally; ventrally the maxillary crests appear as a narrow rim. Supraorbital crests little salient, with small divergent crests in the parietal region; interorbital space slightly concave and granular, with small divergent crests in the canthal apex. Parietal crests poorly marked. Orbitotympanic crests visible, but not expanded. Plane of the tympanum gently sloping. Parotoids not prominent, length 10.5 mm; dorsally with small conical granules. A poorly marked row of granules on tarsus.

Vertebral light line absent, but a light triangle between shoulder and sacral region; with dark)(shaped spots between shoulders, and a sacral M-shaped spot. Belly light.

Dimensions of type (in mm). Head and body 55. Head length 14. Head width 19. Head height 8. Eye 5. Interorbital space 6. Upper eyelid width 4. Elbow to third finger 24. Femur 19. Tibia length 18. Tibia width 6. Heel to fourth toe 29. Foot 20. Female paratype, RNH 10868, same locality, head and body 59 mm. Size range in males 54.5–55 mm, in females 57.5–59 mm.

Juvenile characteristics. Cephalic crests granular.

Distribution. Margarita Island (Guantamare, Porlamar, La Asunción).

Remarks. I name this subspecies in honor of the late Dr. T. Barbour, former Director of the Museum of Comparative Zoology.

Additional material studied. **Venezuela.** *Margarita Island.* La Asunción, USNM 139066–8. Guantamare, RNH 10869 (14 specimens), Porlamar, RNH 10870 (28 specimens), 10871 (4 specimens), 10872 (2 specimens).

Bufo granulosis mirandaribeiroi subsp. nov.

Bufo granulosis Cott, 1926, p. 1159; Myers and Carvalho, 1952, p. 1 (part).

Bufo granulosis granulosis Gallardo, 1957, p. 367 (part).

Holotype. BMNH 1923.11.9.15, male adult, Marajó Island, mouth of Amazon.

Paratypes. BMNH 1923.11.9.16–19, same data.

Description of type. Head elongate, not wide behind the tympanum, depressed. Loreal region sloping and somewhat concave. Snout somewhat prominent and very broad, elongate and sharp. Rostrum sloping. Nostrils elongate and oblique. Cephalic crests smooth, not raised. Canthal crests marked. Subnasal crests visible, but not salient. Suborbital crests close to the lower border of the eye, not meeting postorbitals. Preorbital crests not raised, sloping to the rear. Postorbital crests not raised, near the tympanic anterior border and sloping to the front. Maxillary crests little expanded; in dorsal view the suborbital crests projecting laterally; ventrally, the maxillary crests appear as a narrow rim. Supraorbital crests little salient, with small divergent crests posteriorly; interorbital space somewhat concave, granular, and with small divergent crests on the canthal apex. Parietal crests little visible. Orbitotympanic crests present, but not expanded. Plane of tympanum gently sloping. Parotoids not well marked, length 9 mm; dorsal granules rounded. Dorsal body granules rather flat. Row of tarsal granules scarcely visible. A vertebral light line; general dorsal coloration brown and olive with dark, irregular spots. Belly light.

Dimensions of type (in mm). Head and body 51. Head length 12. Head width 16. Head height 5. Eye 5. Interorbital space 5. Upper eyelid width 4. Elbow to third finger 21. Femur 19. Tibia length 17. Tibia width 5. Heel to fourth toe 28. Foot 18. Female paratype, BMNH 1923.11.9.17, same locality; head and body 61 mm.

Variation. Sometimes suborbital crests somewhat prolonged behind postorbitals. In one specimen from Mato Grosso, vertebral light line not very well marked, very thin. Size range of males 50–52.5 mm, of females 47.5–62 mm.

Distribution. Along the Rio Tocantins and its tributary the Araguaia, on Soure (Marajó Island), on the Upper Araguaia

(Goyaz), Fazenda Montaria on the Rio Araguaia and on Commandante Rodon (Mato Grosso), all localities in Brasil.

Remarks. I name this subspecies in honor of A. Miranda Ribeiro for his work on the amphibians of Brasil.

Literature citations referred to this subspecies. Cott (1926: 1159), Marajó Island; Myers and Carvalho (1952: 1), Rio Tapirape, a tributary of the Araguaia; Cochran (1955: 24–25), Lower Amazonia (USNM 28932–7), and Soure, Marajó Island (AMNH 46196–7) [I have seen these], and also Fazenda Montaria [considered by me (Gallardo, 1957: 367) as probably *B. g. granulosus*].

Material studied. **Brasil.** *Pará.* Soure, on Marajó Island, mouth of Amazon River, AMNH 46196–7; Marajó Island, mouth of Amazon, BMNH 1923.11.9.15–19; “Lower Amazonia,” USNM 28932–7. *Goyaz.* Upper Araguaia, USNM 130179–81. *Mato Grosso.* Fazenda Montaria, Rio Araguaia, MACN 2407 (3 specimens); Commandante Rodon, MCZ 15660.

***Bufo granulosus lutzi* subsp. nov.**

Bufo granulosus Myers and Carvalho, 1952, p. 1 (part).

Bufo granulosus granulosus Cochran, 1955, p. 22 (part), pl. 3, fig. D.

Holotype. MZUM 108908, adult male, Pirapora, Minas Gerais, Brasil.

Paratypes. MZUM 122426–7, same data; MZUM 108912, Barreiras, Bahia, Brasil.

Description of type. Head moderately elongate, wide, depressed. Loreal region sloping and somewhat concave. Snout short, but prominent. Rostrum somewhat sloping. Nostrils elongate and oblique. Cephalic crests smooth and low, sometimes between granular and smooth. Canthal crests not well marked. Subnasal crests little marked. Suborbital crests near the lower border of the eye, not expanded and not meeting suborbitals and postorbitals. Preorbital and postorbital crests but little projecting; postorbital crests sloping forward and close to the anterior border of tympanum. Maxillary crests not expanded; in dorsal view, the sub-

orbital crests projecting laterally; ventrally, the maxillary crests appear as a narrow rim. Supraorbital crests low, without short divergent crests in the parietal region. Interorbital space somewhat concave, granular and without short divergent crests in the canthal apex. Parietal crests not well marked. Orbitotympanic crests not expanded. Plane of tympanum gently sloping. Parotoids somewhat prominent, length 8 mm; dorsal granules rounded. Row of tarsal granulations poorly marked. A vertebral light line; dorsum yellowish with dark longitudinal irregular bands. Belly light.

Dimensions of type (in mm). Head and body 50. Head length 12. Head width 16. Head height 6. Eye 4. Interorbital space 5. Upper eyelid width 4. Elbow to third finger 21. Femur 17. Tibia length 17. Tibia width 6. Heel to fourth toe 26. Foot 18. Female paratype, MZUM 108912, Barreiras, Bahia. Head and body 48 mm.

Variation. Sometimes vertebral light line absent or poorly marked. Size range of males 44–53 mm, of females 48–59 mm.

Juvenile characteristics. Crests granular. Two dark and broken reversed V's on the dorsal medial line. Ventrally with not well-marked dark spots or all light.

Distribution. Along the Rio São Francisco and affluents, excepting the mouth of this river, where *B. g. granulatus* occurs; on Toca de Onça, Barreiras, Bom Jesus da Lapa, Barreiro on Rio Grande (Bahia), Remanso, Januária, São Francisco, Pirapora (Minas Gerais). Also probably in state of Ceará. All localities in Brasil.

Remarks. I name this subspecies in honor of Dr. A. Lutz for his work on the amphibians of Brasil.

Literature citations referred to this subspecies. Myers and Carvalho (1952: 1), Pirapora, Minas Gerais; Cochran (1952: 1), Pirapora (USNM 98244–6), Januária (USNM 98807–11), São Francisco (USNM 98805), all in Minas Gerais [I have seen this material].

Material studied. **Brasil.** Bahia. Toca da Onça, USNM 52613–4. Barreiro on Rio

Grande, MZUM 108912–3. Bom Jesus da Lapa, MZUM 108902, 108910–11 (10 specimens). Minas Gerais. Remanso do Anacleto, MZUM 108909. Januária, MZUM 108905–7 (6 specimens), USNM 98807–11. São Francisco, USNM 98805. Pirapora, MZUM 108903–4, 108908 (5 specimens), USNM 98244–6. Ceará. "Ceara," MCZ 430. *State uncertain.* Amazon Valley, MCZ 10276.

***Bufo granulatus humboldti* subsp. nov.**

Bufo granulatus Cope, 1899, p. 1; Ruthven, 1922, p. 55 (part); Noble, 1924, p. 66; Dunn, 1944, p. 513; Stebbins and Hendrickson, 1959, p. 514.

Holotype. MCZ 24882, adult male, Gualanday, W. of Girardot, Dept. Tolima, Colombia.

Paratype. MCZ 8978, female, Fundación, Colombia.

Description of type. Head short, wide near the eyes, high. Loreal region somewhat sloping. Snout short, but prominent. Rostrum nearly vertical. Nostrils elongate and oblique. Cephalic crests salient and with rippled borders. Canthal crests with smooth borders; a narrow intercanthal space. Subnasal crests scarcely visible. Suborbital crests near the lower border of the eye, expanded and somewhat prolonged beyond the postorbitals. Preorbital crests well marked, somewhat sloping posteriorly. Postorbital crests well marked, near the tympanic anterior border. Maxillary crests with smooth borders, not much expanded; in dorsal view, the suborbital crests projecting laterally; ventrally, the maxillary crests appear as a rather wide rim. Supraorbital crests somewhat projecting; interorbital space somewhat wide and concave, with granules, with very elevated canthal apex and with short divergent crests. Parietal crests hardly visible. Orbitotympanic crests expanded laterally. Tympanum gently sloping laterally and posteriorly. Parotoids subtriangular, not well marked, length 7 mm; with conical rounded dorsal granules. Row of tarsal spinous granules, not well marked. No vertebral light line; dorsum brown with large dark spots, with

a light triangle between shoulders and sacral region; limbs with transverse dark bands. Belly light yellowish.

Dimensions of type (in mm). Head and body 48. Head length 12. Head width 17. Head height 6. Eye 4. Interorbital space 5. Upper eyelid width 4. Elbow to third finger 19. Femur 15. Tibia length 15. Tibia width 5. Heel to fourth toe 26. Foot 17. Female paratype, MCZ 8978, Fundación, Colombia. Head and body 53 mm.

Variation. Rostrum sometimes somewhat sloping. Suborbital crests sometimes poorly marked or not well prolonged beyond postorbitals. Orbitotympanic crests laterally more or less expanded. In some specimens the vertebral light line scarcely visible. Ventral dark spots can be indistinct. Size range of males 35–59 mm, of females 53–63.5 mm.

Juvenile characteristics. Crests granular. Two reversed dark V's on the medial dorsal line, sometimes broken in the apex. Belly light.

Distribution. Panama (Rio Calobre, Isla de Barro Colorado, Arraiján), Colombia and part of Venezuela. In Colombia, it exists, in general, along the Rio Magdalena and also near the Sierra de Santa Marta; Villavieja, Cerbatana (Dept. Huila), Gualanday, Carmen de Apicalá, Mariquita, Honda (Dept. Tolima), Puerto Berrio (Dept. Antioquia), Rio Frío, Rio Cesar, Valledupar, Fundación, Aracataca, Santa Marta, Valencia, Mamatoco, Curumaní (Dept. Magdalena), Sierra Maciuti (Dept. Guajira). But it also occurs to the east of the Cordillera Oriental in Colombia, in El Astillero (Dept. Norte de Santander) and Villavicencio (Dept. Meta), and in Venezuela near San Fernando de Atabapo (*B. g. beebei* also occurs at or near the last locality). Other localities from Venezuela are in general to the northwest of the Cordillera de Mérida: Cua, Lago de Maracaibo, Rio Guasare, El Paito (this last locality very near to Maracay, where *B. g. beebei* is found). Closer to the coast, in the Falcon State, *B. g. beebei* also occurs.

Remarks. Named in honor of the Baron A. von Humboldt for his explorations of South America.

Literature citations referred to this subspecies. Cope (1899: 1), probably from the neighborhood of Bogotá; Ruthven (1922: 55), Santa Marta, Fundación, Aracataca, Valencia, Valledupar [I have seen these specimens which clearly belong to this subspecies, but the specimen from Gaira, Colombia, belongs to *B. g. beebei*]; Noble (1924: 66), Rio Calobre, Panama [material examined: USNM 53739]; Dunn (1944: 513) (considered one of the commonest toads in Colombia); Stebbins and Hendrickson (1959: 514), various Colombian localities [I have seen all their material].

Material studied. **Panama.** Rio Calobre, USNM 53739; Arraiján, ANSP 23391; Barro Colorado Island, Canal Zone, AMNH 22830. **Colombia.** "Colombia," AMNH 20358, 39090, 39127–8. *Guajira.* Sierra Maciuti, USNM 115380; Rio Cesar, USNM 117515. *Magdalena.* Santa Marta, MCZ 8977; Fundación, MCZ 8978, MZUM 45523, 48202–7, 48209 (12 specimens); Curumaní, MCZ 21499; Rio Frío, MCZ 16052, 16054; Aracataca, ANSP 19731; Valencia, Santa Marta Mts., MZUM 54637; Mamatoco, Santa Marta Mts., MZUM 45524, 45526, 48208; Valledupar, Santa Marta Mts., MZUM 54635–6. *Antioquia.* Puerto Berrio, CNHM 30801–4 (5 specimens). *Tolima.* Mariquita, CNHM 81833–4. Gualanday, MZUM 90600 (2 specimens), MCZ 24882–4. Carmen de Apicalá, 400 m, MVZ 41993. Honda, MCZ 16264. *Huila.* Villavieja, 1400 feet, MVZ 63015–8, 63023–4, 5 km N. Villavieja, 1400 feet, MVZ 63019–22, 63025–7 (6 specimens), 6 km SE. Villavieja, 458 m, MVZ 41992 (2 specimens). *Norte de Santander.* El Astillero, Inst. La Salle 250b. **Venezuela.** Lago de Maracaibo, CNHM 3016 (2 specimens). *Aragua.* Cua, CNHM 69780. *Tachira.* Rio Guasare, UCV 3239. *Carabobo.* El Paito, Sur de Valencia, UCV 3167–70. *Territorio Amazonas.* San Fernando de Atabapo, UCV 3171.

Bufo granulosis major Müller and Hellmich

Bufo granulosis major Müller and Hellmich, 1936, pp. 12–13, fig. 3 (type locality San José de Chiquitos, Bolivia); Gallardo, 1957, pp. 364–366, pl. II, figs. 5–7, pl. III, fig. 10, pl. IV, fig. 13.

Bufo d'orbignyi Boettger, 1885, p. 246.

Bufo d'orbignyi Boettger, 1892, p. 39; Andersson, 1906, p. 14.

Bufo granulosis Boulenger, 1894, p. 348 (part); Budgett, 1899, p. 313; Müller and Hellmich, 1936, p. 7 (part); Travassos and Freitas, 1942, p. 283; B. Lutz, 1946, pp. 153, 154; Myers and Carvalho, 1952, p. 1 (part).

Bufo globulosus Berg, 1896, p. 198 (part).

Bufo granulosis d'orbignyi Vellard, 1948, pp. 143, 146; Cei, 1949, pp. 532, 541, 544, pls. I–II; 1950, p. 405 (part); 1953, pp. 512 (part), 515; 1955, p. 291; 1956a, pl. I, fig. 5.

Bufo granulosis granulosis Gallardo, 1957, pp. 366, 367, 368 (part).

Topotype. Adult male, ZSBS 202/26, San José de Chiquitos, Bolivia.

Description. Head short, wide at buccal commissure, high. Loreal region sloping. Snout short, but prominent. Rostrum nearly vertical. Nostrils elongate and oblique. Cephalic crests somewhat raised, with rippled borders, but almost all the lateral crests granular. Canthal crests with smooth borders, intercanthal space rather wide. Subnasal crests distinct and projecting, with smooth borders. Suborbital crests near the lower border of the eye, not laterally expanded, nor prolonged beyond postorbitals. Preorbital crests well marked, scarcely sloping posteriorly. Postorbital crests well marked, sloping a little anteriorly, close to the anterior border of the tympanum. Maxillary crests with smooth borders, laterally expanded, projecting in dorsal view. In ventral view, the maxillary crests appear as a wide rim. Supraorbital crests somewhat projecting; interorbital space concave and wide, granular and with the short divergent crests poorly marked. Parietal crests poorly marked. Orbitotympanic crests generally not well marked. Tympanum distinct, gently sloping. Parotoids thin with poorly marked borders, length 10 mm; dorsal granules conical and horny. A row of spinous

granules on the inner tarsal edge. No vertebral light line; a dorsal dark reticulation. Belly yellowish, light.

Dimensions (in mm). Head and body 55.5. Head length 14. Head width 18. Head height 6. Eye 5. Interorbital space 6. Upper eyelid width 4. Elbow to third finger 23. Femur 20. Tibia length 18. Tibia width 7. Heel to fourth toe 31. Foot 21. Female topotype, ZSBS 202/26, head and body 64.5 mm.

Variation. The suborbital crests may be somewhat laterally expanded and prolonged beyond postorbitals; in this character there is a resemblance to *B. g. fernandezae*. Parietals sometimes scarcely visible. Parotoid dorsal granules rounded (only one specimen). Only one specimen with a vertebral light line. Size range in males 43–70 mm, in females 50–81 mm. Specimens from Puerto Casado (Paraguay), MACN 1756, and from northern Chaco (Paraguay), ZSBS 70/32, are of small size.

Distribution. All the Chacoan region, in Bolivia (San José de Chiquitos, Buena Vista, Tatarenda, Ixiamas, Lago Rogagua), the Paraguayan Chaco (Puerto Vallemi, Puerto Casado, Colonia Mennonita), the Argentinian Chaco (Provinces of Salta, Formosa, Chaco, Santiago del Estero, Santa Fé) and in Brasil in the Pantanal zone of Mato Grosso (Miranda, Pôrto Esperança, Villa Maria, Salobra). In northern Bolivia it meets *B. g. minor* and *B. g. goeldii*. In Pôrto Esperança (Brasil) and in Puerto Casado (Paraguay) it meets *B. g. fernandezae* which extends to the south.

Literature citations referred to this subspecies. In addition to the type series (Müller and Hellmich, 1936: 12) and the material cited by me (Gallardo, 1957: 364) as *granulosus*, the following literature citations are referred to this subspecies:

Boettger (1885: 246; 1892: 39), Paraguay (*Bufo dorbignyi*) [I have now been able to examine these specimens, SM 3148, which I had earlier erroneously considered *B. g. fernandezae* (Gallardo, 1957: 347)]; Boulenger (1894: 348), Asunción. Para-

guay [only BMNH 1894.3.14.161–162, which are probably from the Paraguayan Chaco; two others reported from Asunción are *B. g. fernandezae*, and are probably correctly localized]; Berg (1896: 198), Corrientes, Argentina (*B. globulosus*) [material studied: MACN 3748]; Budgett (1899: 313), Paraguayan Chaco (*B. granulatus*); Andersson (1906: 14), Tatarenda, Bolivia (*B. dorbignyi*) [material studied: ZIUS]; Bertoni (1914: 21), Paraguay [probable]; Müller and Hellmich (1936: 7), San José de Chiquitos, Santa Cruz de la Sierra and northern Chaco [I have seen these, but specimens from San José, Formosa, are *B. g. fernandezae*]; Travassos and Freitas (1942: 283), Salobra, Mato Grosso (*B. granulatus*) [I have studied material from this locality]; B. Lutz (1946: 153, 154), Miranda, Mato Grosso (*B. granulatus*) [material studied: CNHM 67092–3]; Myers and Carvalho (1952: 1), São Luiz de Cáceres, Upper Paraguay River, specimens described as with “short physiognomy and strong infranarial crest” [I have seen one specimen MCSN 29817, from Villa Maria, the same locality that is now called São Luiz de Cáceres]; Gallardo (1957: 366, 367, 368), Puerto Vallemi (MACN 2405–6), Puerto Casado, Paraguay (MACN 1756), referred to as “probably *B. g. granulatus*.”

Material studied. **Paraguay.** “Paraguay,” SM 3148, Asunción, BMNH 1894.3.14.161–162. Colonia Menmonita, 22°10'S, 60°W, Chaco, BMNH 1956.1.2.8–9. Northern Chaco, ZSBS 70/32 (6 specimens). Estancia Guajhó, Puerto Casado, MACN 1756 (5 specimens). Puerto Vallemi, Departamento Concepción, MACN 2405–6. **Bolivia.** San José de Chiquitos, ZSBS 202/26 (3 specimens), CM 36217 (18 specimens), MCZ 29826–43. Buenavista, MCZ 15563 (2 specimens), CM 3824, 4236, MZUM 60548, 60549, 63329, 66522 (9 specimens). Tatarenda, Chaco boliviano, ZIUS (3 specimens). Ixiamas, MZUM 57596 (5 specimens). Lago Rogagua, MZUM 57590 (2 specimens). **Brasil.** *Mato Grosso.* Pôrto Esperança, MZUM 104284. Salobra,

USNM 132907–8, MZUM 104291, 104293. Miranda, MZUM 104289, CNHM 67092–3. Environs of Villa Maria, MCSN 29817. (Argentine specimens recorded in my previous paper are not cited here.)

Bufo granulatus azarai subsp. nov.

Holotype. Adult male, BMNH 1955.1.5–47, Primavera, Upper Paraguay, Paraguay.

Paratypes. AMNH 19877–81, Paraguay.

Description of type. Head short, wide and very depressed. Loreal region sloping and concave. Snout very short, not projecting (hardly visible from the ventral side), but prominent. Rostrum nearly vertical. Nostrils elongate and oblique. Cephalic crests well developed, with smooth or somewhat rippled borders. Canthal crests with smooth borders. Subnasal crests distinct. Suborbital crests well separated from the lower border of the eye, forming a small projecting arch, expanded laterally and prolonged beyond postorbitals. Preorbital crests marked. Postorbital crests marked and somewhat separated from the tympanum. Maxillary crests very much expanded laterally; seen from above, the maxillaries project laterally; ventrally, the maxillaries appear as an expanded rim. Supraorbital crests projecting, with short divergent crests in the parietal region; interorbital space concave and very wide, granular and with short divergent crests on the canthal apex. Parietal crests marked. Orbitotympanic crests with thick border. Tympanum visible, gently sloping. Parotoids not prominent, length 7 mm; dorsally with flat granules. Granules on the dorsum rather smooth. The row of granules on the inner tarsal edge indistinct. A vertebral light line, thin and irregular; dorsal coloration generally dark gray or brown, with scattered, small darker spots. Belly with dark spots.

Dimensions of type (in mm). Head and body 50. Head length 11. Head width 15.5. Head height 5. Eye 3.5. Interorbital space 7. Upper eyelid width 3. Elbow to third finger 17. Femur 14. Tibia length 14. Tibia width 5. Heel to fourth toe 20. Foot 15.

Female paratype, AMNH 19878, Paraguay. Head and body 57 mm.

Variation. Seen from above, the suborbital crests sometimes project more than the maxillaries. Vertebral light line generally absent or only indicated. Ventrally sometimes without spots.

Juvenile characters. Granulated crests, not prominent, similar to those of juveniles in other subspecies. Dorsal coloration gray with darker spots in the shape of two broken inverse V's, on the dorsal median line.

Distribution. Near the rivers that begin in the Sierras de Maracajú and Amambay on the Paraguayan–Brazilian border; Primavera (24°30'S, 56°40'W.) in Paraguay and Maracajú (southern Mato Grosso) in Brasil. These Sierras make a “divortium aquarum” between the Paraná and Paraguay rivers. To the west of the locality of Maracajú, in Miranda, *B. g. major* occurs, while to the west of Primavera, *B. g. fernandezae* occurs on the banks of the Paraguay River.

Remarks. I name this subspecies in honor of the Spanish naturalist Felix de Azara, for his work on the fauna of Paraguay.

Material studied. **Paraguay.** Primavera, 24°30'S, 56°40'W, Alto Paraguay, BMNH 1955.1.5.45–47 (3 specimens); “Paraguay,” AMNH 19877–81. **Brasil.** Mato Grosso. Maracajú, USNM 107701.

Bufo granulatus pygmaeus Myers and Carvalho
Bufo pygmaeus Myers and Carvalho, 1952, p. 1
(type locality São João da Barra, Estado de Rio de Janeiro, Brasil).

Description of paratype. USNM 132357, adult male, São João da Barra. Head moderately elongate, wide at the angle of the mouth, and depressed. Loreal region sloping. Snout short and prominent. Rostrum somewhat sloping backwards. Nostrils elongate and oblique. Cephalic crests with smooth or somewhat rippled borders. Subnasal crests distinct. Suborbital crests near the lower border of the eye, not much expanded laterally, prolonged beyond the postorbitals. Preorbital crests visible, sloping forward (not vertical) and far from the

anterior border of the tympanum. Maxillary crests scarcely expanded; in dorsal view the maxillaries project laterally; ventrally, the maxillaries appear as a somewhat expanded rim. Supraorbital crests somewhat raised; interorbital space somewhat concave and granular. Parietal crests marked. Orbito-tympanic crests well marked. Plane of tympanum gently sloping. Parotoids not prominent, length 4 mm; dorsally with smooth granules. A row of tarsal granules not well marked. A vertebral light line; dorsally large dark and light spots. Belly light gray.

Dimensions of specimen described (in mm). Head and body 29. Head length 8. Head width 11. Head height 4. Eye 3. Interorbital space 3. Upper eyelid width 3. Elbow to the third finger 13. Femur 9. Tibia length 9. Tibia width 3. Heel to fourth toe 15.5. Foot 10.

Variation. Only one specimen without vertebral light line among thirteen examined. Five specimens with black ventral spots. Size range, according to Myers and Carvalho (1952: 2) of males 25–41 mm, of females 31–42 mm.

Distribution. Myers and Carvalho (1952: 1) say this form is distributed along the littoral region of the state of Rio de Janeiro (São João da Barra on the mouth of the Rio Parahyba and Restinga da Marambaia). The other subspecies geographically close are: *B. g. lutzii* to the north in Pirapora (Minas Gerais) and *B. g. dorbignyi* to the southwest in Alto de Serra (São Paulo).

Remarks. I believe this form can be considered as a subspecies of *B. granulatus* and that it is close to other subspecies occurring in eastern Brasil. I have studied 13 paratypes of this subspecies, but I have not seen the specimens which Cei (1956b: 324) reported from Ituzzaingó, Corrientes, Argentina. I think it is probable that the latter are *B. g. fernandezae*, which has some characters in common with *pygmaeus* and sometimes is of small size.

Material studied. **Brasil.** Rio de Janeiro. São João da Barra, USNM 132356–7, MZUM 104960, 115657 (11 specimens).

***Bufo granulosus fernandezae* Gallardo**

Bufo granulosus fernandezae Gallardo, 1957, pp. 347–358, pl. 1, figs. 1, 2; pl. III, fig. 9; pl. IV, fig. 12; pl. V, figs. 14–16. (Type locality Bella Vista, Provincia de Buenos Aires, Argentina.)

Bufo granulosus Boulenger, 1889, p. 247; 1894, p. 348 (part); 1898b, p. 126; Peracca, 1895, p. 29; Müller and Hellmich, 1936, p. 7 (part); Gallardo, 1958, pp. 291, 298, 300.

Bufo d'orbignii Burmeister, 1861, vol. 1, p. 481; vol. 2, p. 533.

Bufo d'orbignyi Müller, 1882, p. 127 (part), p. 138 (part), p. 143; Fernandez, 1926, p. 308, pl. II, fig. 4; pl. III, fig. 4; pl. IV, fig. 1 (part), figs. 4–5; Cei, 1953, p. 521.

Bufo Dorbignyi Berg, 1896, pp. 151, 154, 196 (part).

Bufo granulosus d'orbignyi Cei, 1953, p. 521 (part); Cei and Pierotti, 1955, pp. 11, 12, 14; Ringuelet and Aramburni, 1957, p. 25 (part).

Description of type. MACN 10.334, adult male, Bella Vista, Provincia de Buenos Aires, Argentina. Head short, wide and high. Loreal region somewhat sloping. Snout short though somewhat projecting, prominent in ventral view. Rostrum nearly vertical. Nostrils elongate and little oblique. Cephalic crests high, with smooth borders or somewhat rippled. Canthal crests well developed. Subnasal crests distinct. Suborbital crests rather far from the lower border of the eye, expanded laterally and prolonged beyond the postorbitals. Preorbital and postorbital crests visible, but not very prominent; postorbital crests far from the lower border of the eye, expanded laterally and prolonged beyond the postorbitals. Preorbital and postorbital crests visible, but not very prominent; postorbital crests far from the anterior border of the tympanum. Maxillary crests somewhat expanded; in dorsal view suborbital crests project laterally; ventrally, the maxillaries appear as a wide rim. Supraorbital crests developed, but not covering the upper eyelid; interorbital space somewhat concave and deep, somewhat granular. Parietals well marked. Orbito-tympanic crests well developed. Tympanum visible, anterior border somewhat prominent, nearly vertical. Parotoids subtriangular,

somewhat elongate (10 mm), lower border not well marked; dorsally with flat granules. No row of granules on the inner tarsal edge. Vertebral light line with an interscapular expansion; ground color blackish with greenish spots. Belly grayish yellow with dark spots.

Dimensions of type (in mm). Head and body 60. Head length 15.5. Head width 20. Head height 8. Interorbital space 5.5. Upper eyelid width 4. Elbow to third finger 25. Femur 21. Tibia length 19. Heel to fourth toe 32.5. Foot 22. Female paratype (allotype) MACN 10.355 same locality. Head and body 80 mm.

Variation. Parietal crests little marked or only one side marked. Suborbitals prolonged sometimes only on one side of the head. Specimens from Pôrto Esperança (where the subspecies meets *B. g. major*) without vertebral light line or with only the interscapular expansion. Size range of males 36–65 mm, females 68–80 mm.

Juvenile characters. Dorsum with five dark spots in pentagonal disposition. Belly light or with dark spots.

Distribution. Along the Paraguay, Paraná, Uruguay (Argentine side) and La Plata rivers, in general not far from the banks; thus from Pôrto Esperança in Mato Grosso (Brasil) and Puerto 14 de Mayo, Bahía Negra (Paraguay) to near La Plata, Province of Buenos Aires (Argentina). In Uruguay from Nueva Palmira to Montevideo.

Literature citations referred to this subspecies. Burmeister (1861, 1: 481, and 2: 533), Paraná, Entre Rios, Argentina (*B. dorbignyi*); Müller (1882: 127, 138, 143), Leones, Córdoba, Argentina (*B. dorbignyi*) [I studied material from this locality for my earlier work]; Boulenger (1889: 247), Resistencia, Chaco, Argentina [material studied: MCSN 29611]; Boulenger (1894: 348), Asunción, Paraguay [material examined: BMNH 1894.3.14.159–160]; Boulenger (1898b: 126), Puerto 14 de Mayo, Paraguay [material examined: MCSN 30492]; Peracca (1895: 29), Resistencia, Argen-

Asunción, Paraguay [material from Asunción studied: IMZUT 1084]; Berg (1896: 151, 154, 196), Corrientes, Santa Fé and Entre Ríos, Argentina, and some of his specimens from Buenos Aires, Argentina, and from the Republica de Uruguay; Müller and Hellmich (1936: 7), San José, Formosa (*B. g. granulatus*) [material studied: ZSBS 152/28]; Cochran (1955: 26), La Plata (USNM 22750), Montevideo, Uruguay (USNM 65576, 70618) (*B. g. dorbignyi*) [USNM 70618 is one of the specimens reported by Metcalf (1940: 486, 487, 489, 563) as *B. dorbignyi*]; Cei and Pierotti (1955: 11, 12, 14), Paraná Delta; Gallardo (1958: 291, 298, 300), typical locality (a paper written before the subspecies was described).

Remarks. The intermediate position of this subspecies becomes evident from an analysis of its synonymy, since what the European authors generally reported as *B. granulatus* was, to Argentinians and Americans, *B. dorbignyi*.

Material studied. **Argentina.** "Provincia de Buenos Aires," AMNH 11962; La Plata, CNHM 9691-3, USNM 22750; Isla Ella, Río Paraná, MZUM 76113; Gualaguaychú, Entre Ríos, MACN 7114 (2 specimens); Colonia Resistencia, Chaco, MCSN 29611 (6 specimens), MCSN 29915; San José, Formosa, ZSBS 152/28 (18 specimens). **Uruguay.** Montevideo, MZUM 59011 (2 specimens), BMNH 1923.12.4.11-13, USNM 65576, 70618. **Paraguay.** "Paraguay," MCZ 2237; Río Pilcomayo, CNHM 42294; Colonia Nueva Italia, CNHM 42295-7, AMNH 50672-5, MCZ 25801-3; Asunción, IMZUT 1084 (10 specimens), BMNH 1930.11.27.-293-7, 1894.3.14.159-160; Bahía Negra, Puerto 14 de Mayo, MCSN 30492. **Brasil.** Pôrto Esperança, Mato Grosso, MZUM 104271, 104283 (3 specimens).

Bufo granulatus dorbignyi Duméril and Bibron

Bufo d'Orbignyi Duméril and Bibron, 1841, p. 697 (type locality Montevideo); Hensel, 1867, p. 141; Müller, 1882, pp. 127, 138 (part); Boulenger, 1885b, p. 296; Nieden, 1923, pp. 76, 143

(part), fig. 191; Lutz, 1934, p. 123 (part), pl. XXVII, figs. 1-1a.

Bufo Orbignyi Bibron, 1847, p. 11.

Bufo D'Orbignyi Bibron, 1847, pl. 15, figs. 5-7; Marelli, 1931, p. 201 (part).

Bufo d'orbignyi Günther, 1858, p. 67 (part); Boulenger, 1882, pp. 285, 322, figs.: Baumann, 1912, pp. 143, 146, 154 (part); Miranda Ribeiro, 1926, p. 132 (part); Vanzolini, 1953, p. 125; Klingelhöffer and Scherpner, 1956, p. 160, fig. 127.

Bufo dorbignyi Cope, 1885, p. 185.

Bufo D'Orbignyi Boulenger, 1885a, p. 196.

Bufo Dorbignyi Boulenger, 1886, pp. 442, 443; Berg, 1896, pp. 151, 154, 196 (part); Marelli, 1924, p. 586 (part); Mello-Leitão, 1937, p. 342 (part).

Chilophryne d'Orbignyi Fitzinger, 1843, p. 32.

Chilophryne d'orbignyi Cope, 1862, p. 358.

Chilophryne D'orbignyi Jiménez de la Espada, 1875, p. 188.

Bufo granulatus d'orbignyi Cei, 1953, pp. 512, 521 (part); Cochran, 1955, p. 25 (part), pl. 3, figs. G-I; pl. 34, fig. F; Gallardo, 1957, p. 358, pl. I, figs. 3-4; pl. III, fig. 8; pl. IV, fig. 11; Ringuelet and Aramburu, 1957, p. 25 (part).

Redescription of type. MNHN 4960, adult female, Montevideo, Uruguay. Head short, wide, and high. Loreal region nearly vertical. Snout very short, barely seen ventrally. Rostrum nearly vertical, rounded. Nostrils elongate and little oblique. Cephalic crests very high, with smooth or somewhat rippled borders. Canthal crests very high. Subnasal crests distinctly visible. Suborbital crests not marked. Preorbital crests well defined. Postorbital crests very poorly marked. Maxillary crests much expanded; in dorsal view the maxillaries project laterally; ventrally, the maxillaries appear as a very expanded rim. Supraorbital crests very well developed, covering laterally part of the upper eyelids resembling an extra eyelid; interorbital space very concave and deep, practically without granules. Parietals well marked. Orbitotympanic crests very high. Tympanum in general not well marked; nearly vertical. Parotoids subtriangular, with lower border not well marked, length 7 mm; dorsal granules flat. No row of granules on inner tarsal edge. A verte-

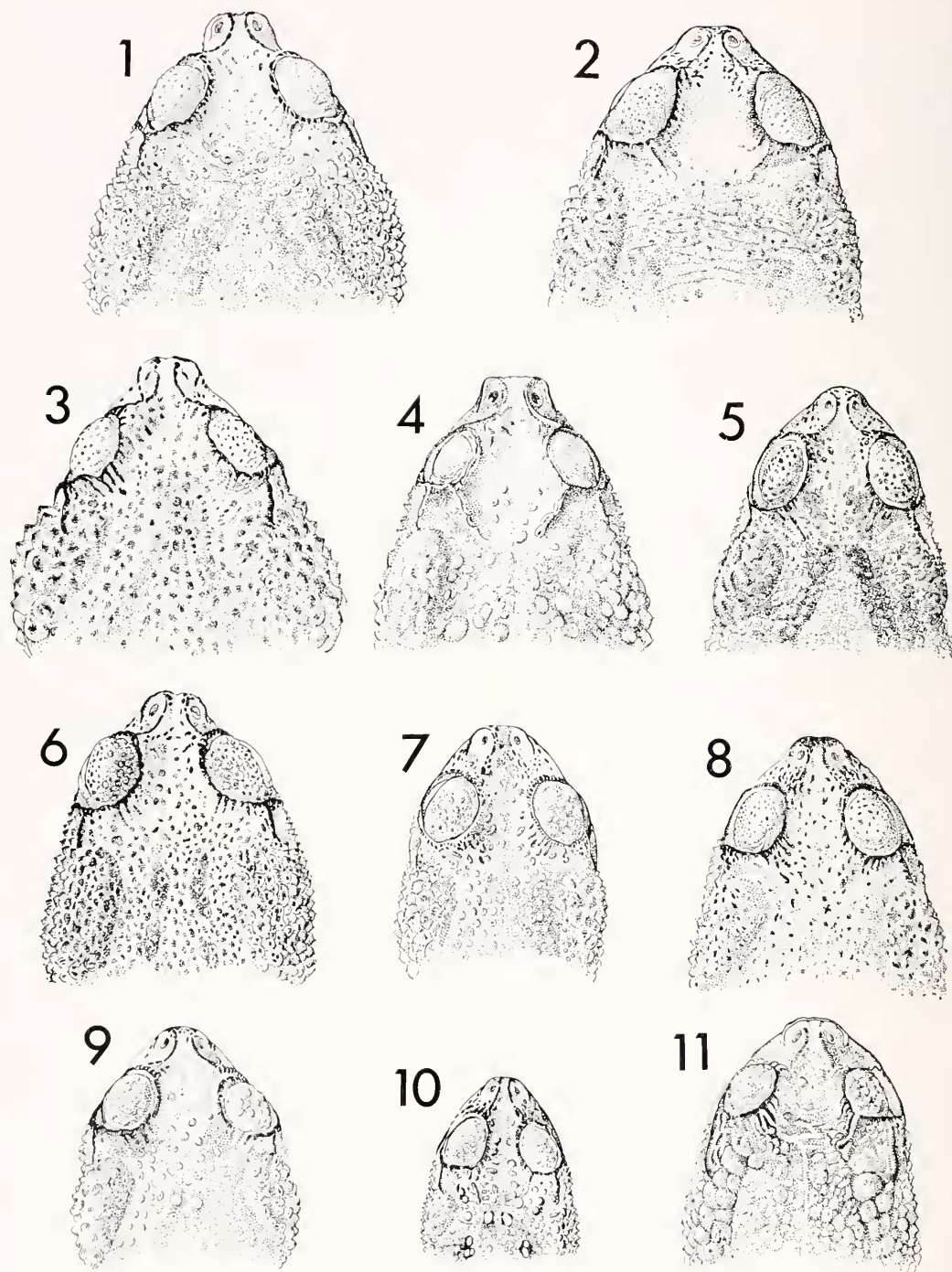


Fig. 1. Dorsal views of heads of *Bufo granulosus* subspecies. 1. *Bufo g. granulosus*, USNM 97107. 2. *B. g. goeldii*, MZUM 64528. 3. *B. g. merianae*, AMNH 46531. 4. *B. g. minor*, MCZ 10089. 5. *B. g. beebei*, AMNH 55774. 6. *B. g. barbaui*, RNH 10867. 7. *B. g. mirandaribeirai*, BMNH 1923.11.9.15. 8. *B. g. lutzii*, MZUM 108908. 9. *B. g. humboldti*, MCZ 24882. 10. *B. g. pygmaeus*, USNM 132357. 11. *B. g. azarai*, BMNH 1955.1.5.47.

bral light line; dorsum with large dark spots; dark bands on limbs. Belly grayish yellow.

Dimensions (in mm). Head and body 66. Head length 14. Head width 21. Head height 7.5. Eye 5. Interorbital space 9. Upper eyelid width 3. Elbow to third finger 24. Femur 17. Tibia length 17.5. Tibia width 7. Heel to fourth toe 29.5. Foot 21.5.

Variation. Specimens from marginal zones of the subspecies area, as Pôrto Alegre and Montevideo, show some variation of the crests: supraorbitals rather low; parietals more or less distinct; suborbitals very variable: (a) only a feeble indication not prolonged behind postorbitals; (b) visible, separated from lower border of eye but neither expanded nor prolonged; (c) present, only prolonged on one side of head; maxillaries somewhat broken; postorbitals obscurely visible. Other variations are: tympanum very distinct (well separated from postorbitals); interorbital space with granules; vertebral light line expanded in interocular and interscapular regions. Size range: males 44.5–57 mm, females 51.5–103 mm. This last specimen comes from Fray Bentos, Uruguay, and it is the largest specimen of the species that I have seen.

Distribution. This subspecies is found in Uruguay, probably over most of the country except the coastal portion from Nueva Palmira (upon the Uruguay River banks) to Montevideo; it occurs also in Fray Bentos (although on the Argentine side of the Uruguay River, in Gualguaychú, *B. g. fernandezae* occurs) and in San Carlos (east of Montevideo). Some specimens from Montevideo are intermediate between this subspecies and *B. g. fernandezae*: specimens also with intermediate characters occur in Pôrto Alegre and Alto da Serra, in Brasil. In Argentina it is found in Buenos Aires Province from Chascomús and Saladillo to D'Orbigny (Partido de Coronel Suarez) and to the east it occurs in Mar del Plata upon the Atlantic coast.

Remarks. I have seen the type of *B. dorbignyi*, MNHN 4960. The catalogue data for the specimen mention the locality,

Montevideo, and collector, A. D'Orbigny (according to a letter from Dr. J. Guibé from the Muséum National d'Histoire Naturelle, Paris). For reasons previously explained (Gallardo, 1957: 340–342) I think that the true locality is Maldonado, Uruguay.

Literature citations referred to this subspecies. Hensel (1867: 141), Pôrto Alegre, Rio Grande do Sul, [material studied: ZMB 6803]; Cope (1885: 185), Rio Grande do Sul, probably São João do Monte Negro; Boulenger (1885a: 196, 1885b: 296, 1886: 442, 443), Rio Grande do Sul; Lutz (1934, pl. XXVII, figs. 1–1a), São Francisco de Paulo, Rio Grande do Sul, Brasil, Buenos Aires, Argentina. [The latter specimen is figured without a suborbital crest.] Cochran (1955: 25, pl. 3, figs. G–I), Alto da Serra, São Paulo, Brasil [material examined: USNM 102314, and the type (photograph, pl. 34, fig. F), also USNM 97188 from Buenos Aires Province, Argentina]. (Of the other specimens referred by Cochran to *B. g. dorbignyi*, USNM 65593–4, Malvin, Uruguay, and USNM 65578–80, Montevideo, Uruguay, are juvenile *Bufo arenarum*. Those still remaining have been cited above under *B. g. fernandezae*.) Klingelhöffer and Scherpner (1956: 160, fig. 127), photo of one specimen without a suborbital crest from southern Brasil. Gallardo (1957: 362, 363), Buenos Aires Province, Argentina (Libres des Sur, Chascomús, Rosas, Casalins, Tandil, Santo Domingo, Juancho, D'Orbigny, Cazón), San Carlos, Uruguay, and Pôrto Alegre, Brasil.

Material studied. **Uruguay.** Montevideo, MNHN 4960 type, MNHN 4959 (4 specimens). San Carlos, CNHM 9524–5. Near Fray Bentos, MCZ 1541 (2 specimens). **Argentina.** "Provincia de Buenos Aires," MZUM 94075, USNM 97188. Mar del Plata, Provincia de Buenos Aires, AMNH 33991–7, 34077–82. **Brasil.** *Rio Grande do Sul.* Pôrto Alegre, SM 21630, 30485, 21334–5, ZMB 6803 (4 specimens). *São Paulo.* Alto da Serra, USNM 102314.

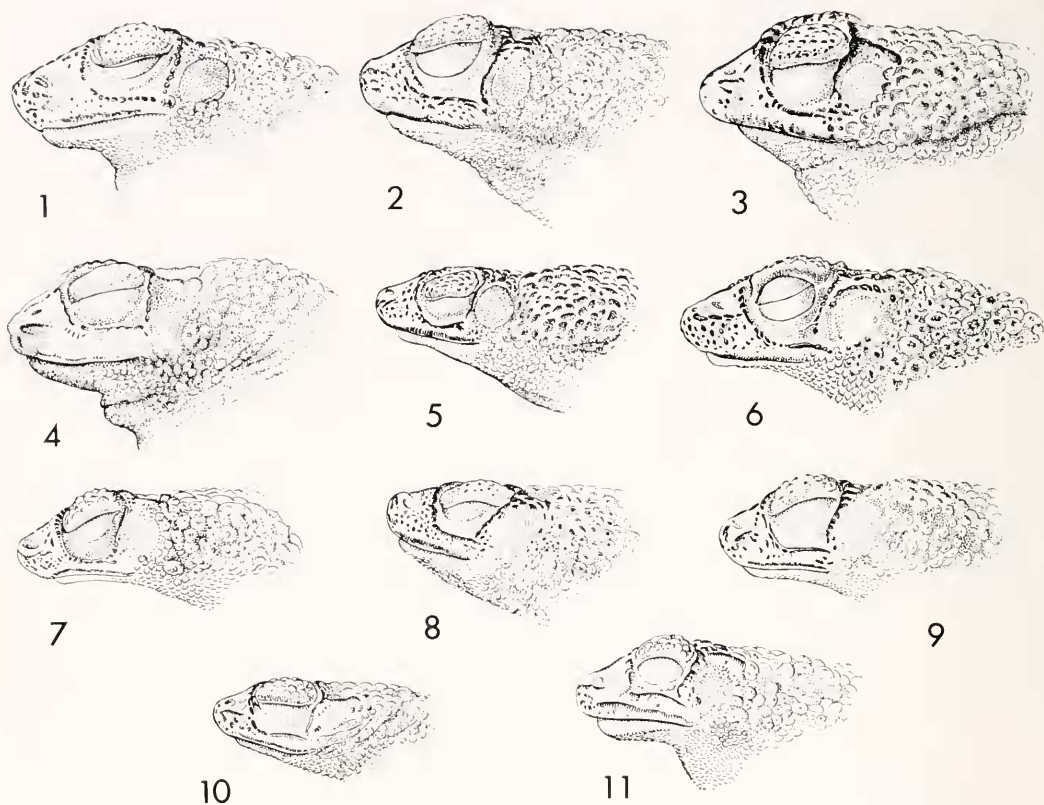


Fig. 2. Lateral views of heads of *Bufo granulosus* subspecies. 1. *B. g. granulosus*, USNM 97107. 2. *B. g. goeldii*, MZUM 64528. 3. *B. g. merianae*, AMNH 46531. 4. *B. g. minor*, MCZ 10089. 5. *B. g. beebei*, AMNH 55774. 6. *B. g. barbouri*, RNH 10867. 7. *B. g. mirandaribeiroi*, BMNH 1923.11.9.15. 8. *B. g. lutzi*, MZUM 108908. 9. *B. g. humboldtii*, MCZ 24882. 10. *B. g. pygmaeus*, USNM 132357. 11. *B. g. azarai*, BMNH 1955.1.5.47.

DISCUSSION

When the different subspecies of *B. granulosus* are compared, two distinct types of heads are noticed: one, high, short and wide, and the other depressed, in general elongate, and narrow. To the first group belong: *B. g. granulosus*, *B. g. goeldii*, *B. g. merianae*, *B. g. minor*, *B. g. major*, *B. g. fernandezae*, *B. g. dorbignyi*, and to the second: *B. g. beebei*, *B. g. lutzi*, *B. g. mirandaribeiroi*, *B. g. barbouri*, *B. g. pygmaeus*, *B. g. azarai*.

The distribution of the subspecies with depressed heads is not continuous; instead, between *B. g. beebei* and the others of this series there are *B. g. merianae* and *B. g. goeldii* with high, short and wide heads.

The development of the crests varies among the subspecies. In some they are low and granular, in others they have rippled borders, and in some others they are considerably raised, as in *B. g. fernandezae*, *B. g. dorbignyi*, *B. g. merianae*, *B. g. azarai*. The degree of expansion of the maxillary crests varies considerably from one subspecies to another: in *B. g. granulosus* they are not expanded; in the subspecies of northern South America they are better marked, but achieve their greatest development in certain of the southern subspecies, i.e., *B. g. major*, *B. g. fernandezae*, *B. g. azarai* and especially in *B. g. dorbignyi*. The dorsal granules on the parotoids are rounded and flat in the subspecies of northeast and

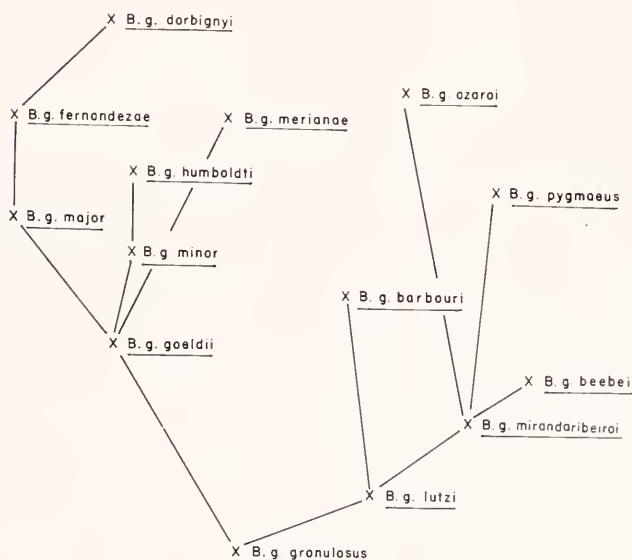
southeast South America, but rather conical in *B. g. humboldti* from Colombia and Panama and very definitely conical in *B. g. major* of the Chacoan region.

It is not possible to arrange the subspecies of *B. granulatus* linearly, but they can be located on a branched scheme in which equivalent levels correspond to equivalent development in the cephalic crests. In such a diagram, which has only the object of providing a means of comparing the known subspecies, *B. g. granulatus* may be located at the base, as a subspecies with a short head, low and granular crests, and maxillary crests not expanded. This would lead, on one side, to *B. g. lutzi* (with somewhat elongate head, intermediate crests, maxillaries with a minimum of expansion), and, on the other side, to *B. g. goeldii* (with short and wide head, smooth and low crests, maxillaries somewhat expanded).

From *B. g. lutzi* would be derived *B. g. barbouri* (with intermediate head type, medium degree of prominence of the crests, borders scarcely rippled, maxillaries little

expanded) and *B. g. mirandaribeiroi* (with head elongate and depressed, crests smooth and not elevated, maxillaries little expanded). From the latter would be derived: *B. g. beebei* (with elongate and depressed head, cephalic crests not very high and smooth, maxillaries barely expanded); *B. g. pygmaeus* (form of small size, head somewhat expanded and depressed, cephalic crests with smooth or somewhat rippled borders and relatively high, maxillaries somewhat expanded and suborbitals beyond postorbitals); *B. g. azarai* (head wide and depressed, with well developed cephalic crests, with smooth or somewhat rippled borders, maxillaries much expanded laterally, suborbitals also expanded and prolonged beyond postorbitals). These two latter subspecies are forms convergent to *B. g. fernandezae*, which has suborbitals expanded and prolonged beyond postorbitals.

From *B. g. goeldii* there could be derived *B. g. merianae* (with head short, laterally expanded and high, cephalic crests projecting and in general with rippled borders,



DENDROGRAM OF THE RELATIONSHIPS OF THE
SUBSPECIES OF *Bufo granulatus* Spix

maxillaries somewhat expanded and prolonged beyond postorbitals—convergent to *B. g. fernandezae*); *B. g. minor* (with short and high head, cephalic crests somewhat projecting and with generally rippled borders, maxillaries somewhat expanded) and from this *B. g. humboldti* (with head short, wide and high, projecting cephalic crests with rippled borders, maxillaries not very expanded, suborbitals expanded and somewhat prolonged beyond postorbitals); *B. g. major* (with head short, wide and high, cephalic crests with rippled or granular borders, somewhat projecting, maxillaries laterally expanded) and from this subspecies one could pass to *B. g. fernandezae* (with head short, wide and high, cephalic crests high, with smooth or little rippled borders, maxillaries somewhat expanded, suborbitals laterally expanded and prolonged beyond postorbitals). From *B. g. fernandezae* it is possible to pass to *B. g. dorbignyi* (with head short, wide and high, cephalic crests very high and with smooth or little rippled borders, maxillaries very wide). In this subspecies the supraorbital crests show maximum prominence as do the maxillaries, but the suborbitals and postorbitals are practically nonexistent.

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TABLE 1

	<i>granulosus</i>	<i>goeldii</i>	<i>merianae</i>	<i>minor</i>	<i>beebei</i>	<i>barbouri</i>	<i>miranda- ribetoi</i>
Head	Short, wide, high	Short, wide in buccal commissure, high	Short, wide in buccal commissure, high	Short, wide, high	Elongate, not wide, depressed	Moderately elongate, somewhat wide, depressed	Elongate, not wide, depressed
Loreal region	Nearly vertical	Nearly vertical	Nearly vertical	Somewhat concave	Sloping	Slightly sloping	Sloping, somewhat concave
Snout	Short	Very short	Short	Short	Elongate	Short, wide	Very broad, elongate
Rostrum	Slightly sloping	Nearly vertical	Nearly vertical	Nearly vertical	Sloping	Somewhat sloping	Sloping
Nostrils	Somewhat oblique	Oblique	Somewhat oblique	Somewhat oblique	Oblique	Oblique	Oblique
Cephalic crests	Low, granular or scalloped	Moderately developed, generally between smooth and rippled	Projecting, generally rippled	Somewhat projecting, generally rippled	Not very prominent, smooth or somewhat rippled	Somewhat elevated, generally lightly rippled	Not raised, smooth
Subnasal crests	Scarcely noticeable	Well defined, smooth	Noticeable	Projecting	Somewhat noticeable	Noticeable	Not projecting
Canthal crests	Granular	Smooth	Smooth	Smooth	Smooth	Smooth	Marked
Suborbitals, distance eye to eye	Very close; not prolonged	Little separated, somewhat expanded; not prolonged	Little separated; prolonged	Close; not prolonged	Close; prolonged by granules	Close; reaching a little beyond	Close; not prolonged
Preorbital crests	Well defined	Sloping	Sloping, with postorbitals and supra- orbitals making a rim around eye	Somewhat projecting	Projecting, a small flange in front of eye, sloping	Not very salient, sloping	Not raised, sloping
Postorbital crests	Well defined. Close to tympanum. Sloping	Close to tympanum. Sloping	Close to tympanum	Somewhat projecting. Close to tympanum	Close to tympanum. Sloping	Separated from tympanum	Not raised, near tympanum, sloping

TABLE 1. *Continued*

<i>lutzi</i>	<i>humboldti</i>	<i>major</i>	<i>azarai</i>	<i>pygmaeus</i>	<i>fernandezae</i>	<i>dorbignyi</i>
Moderately elongate, wide, depressed	Short, wide near eyes, high	Short, wide at buccal commissure, high	Short, wide, very depressed	Moderately elongate, wide at buccal commissure	Short, wide, high	Short, wide, high
Sloping, somewhat concave	Somewhat sloping	Sloping	Sloping, concave	Sloping	Somewhat sloping	Nearly vertical
Short	Short	Short	Very short	Short	Short	Very short
Somewhat sloping	Nearly vertical	Nearly vertical	Nearly vertical	Somewhat sloping	Nearly vertical	Nearly vertical
Oblique	Oblique	Oblique	Oblique	Oblique	Slightly oblique	Slightly oblique
Low, smooth or between granular and smooth	Salient, rippled	Somewhat raised, rippled or granular	Well developed, smooth or somewhat rippled	Relatively raised, smooth or somewhat rippled	High. Smooth or somewhat rippled	Very high. Smooth or somewhat rippled
Little marked	Scarcely visible	Quite visible, projecting	Visible	Visible	Visible	Quite visible
Not well marked	Smooth, a narrow intercanthal area	Smooth, a rather wide intercanthal area	Smooth	Smooth	Well developed	Very high
Close; not expanded or prolonged	Close; expanded, somewhat prolonged	Close; not expanded or prolonged	Well separated, small arch, expanded, prolonged	Close; not very expanded, prolonged	Rather distant. Expanded, prolonged	Not well marked
Slightly projecting	Well marked, somewhat sloping	Well marked, scarcely sloping	Marked	Somewhat sloping	Visible but not very prominent	Well defined
Slightly projecting, near tympanum, sloping	Well marked, near tympanum	Well marked, near tympanum, slightly sloping	Marked, somewhat separated from tympanum	Far from tympanum, sloping	Not very prominent. Far from tympanum	Very poorly marked

TABLE 2

	<i>granulosus</i>	<i>goeldii</i>	<i>merianae</i>	<i>minor</i>	<i>beebei</i>	<i>barboursi</i>	<i>miranda- ribeiroi</i>
Maxillary crests	Not expanded	Somewhat expanded	Somewhat expanded	Somewhat expanded	Scarcely expanded	Little expanded	Little expanded
Projecting laterally in dorsal view	Suborbitals	Maxillaries (slightly)	Suborbitals	Maxillaries (slightly)	Suborbitals	Suborbitals	Suborbitals
Maxillary ventral rim	Absent	Present	Present	Present	Narrow	Narrow	Narrow
Supra-orbital crests	Low	Not very high	Projecting, rippled, short oblique crests in parietal region	Only slightly projecting	Slightly raised, short divergent crests in parietal region	Slightly projecting, short divergent crests in parietal region	Slightly projecting. Short divergent crests in the parietal region
Inter-orbital space	Slightly concave, granular	Little concavity, granular, not very wide. Short crests at the canthal apex	Concave, granular. Short divergent crests at the canthal apex	Concave, granular. Short divergent crests at the canthal apex	Somewhat concave, granular. Short crests at the canthal apex	Slightly concave, granular. Short crests at the canthal apex	Somewhat concave, granular. Short crests at canthal apex
Parietal crests	Scarcely or not marked	Marked	Scarcely marked	Marked	Very short	Poorly marked	Slightly noticeable
Orbito-tympanic crests	Not well marked	Well marked	Marked	Marked	Well marked	Marked	Not expanded
Tympanum	Oblique	Oblique	Nearly vertical	Nearly vertical	Oblique	Slightly oblique	Gently sloping
Parotoids	Not prominent. Dorsal granules convex	Not prominent. Dorsal granules rounded	Large, not very prominent. Dorsal granules rounded	Prominent, lateral borders not well marked. Dorsal granules rounded, horny	Large. Dorsal granules large, rounded, flat	Not prominent. Dorsal granules small, conical	Not well marked. Dorsal granules rounded
Row of granules at tarsal inner edge	Present	Present	Present	Present	Present	Poorly marked	Hardly noticeable
Vertebral light line	Absent	Absent	Absent	Absent	Absent or just visible anteriorly	Absent	Present

TABLE 2. Continued

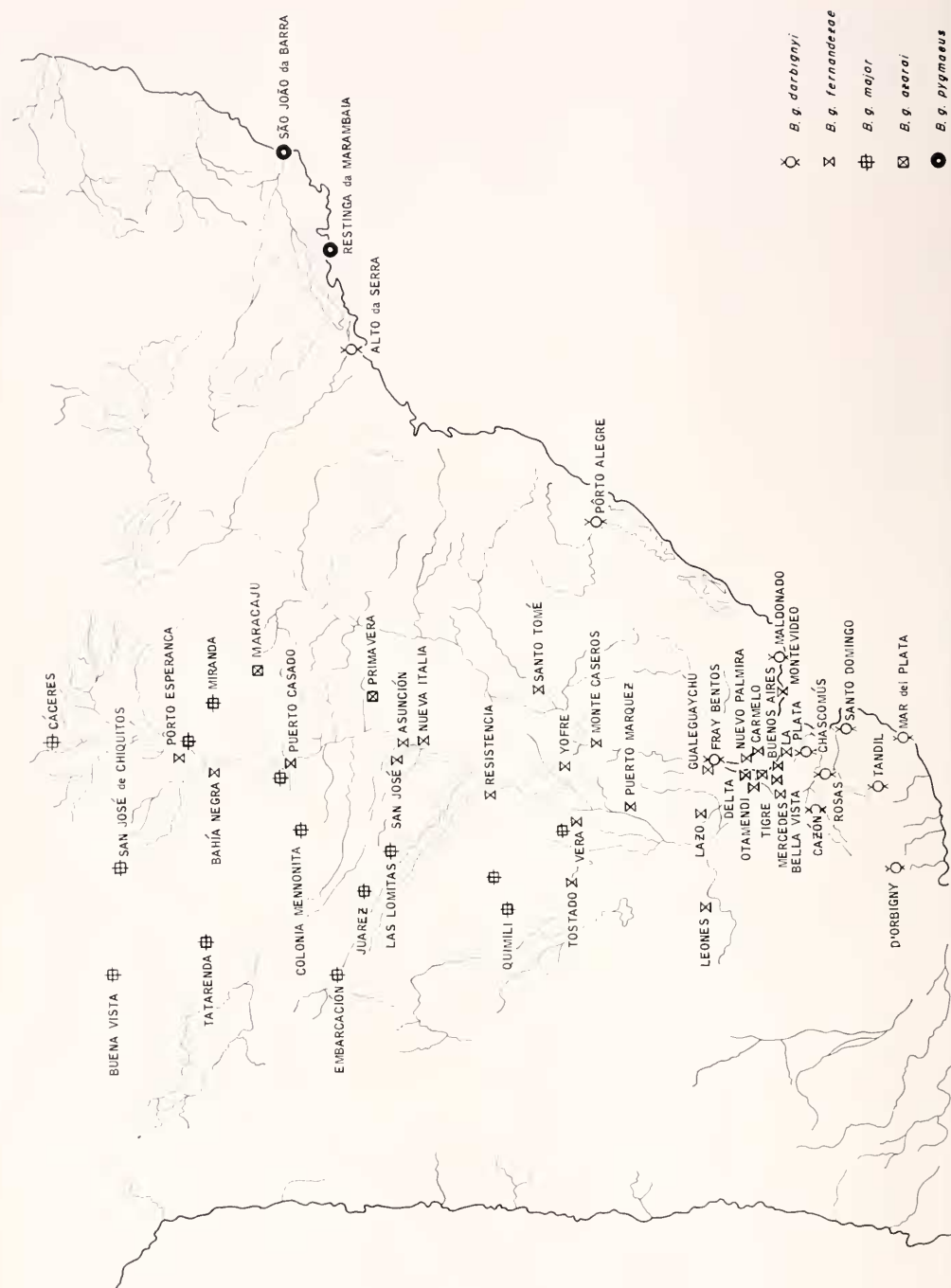
<i>lutzi</i>	<i>humboldti</i>	<i>major</i>	<i>azarai</i>	<i>pygmacus</i>	<i>fernandezae</i>	<i>dorbignyi</i>
Not expanded	Not very expanded	Laterally expanded	Very much expanded	Scarcely expanded	Somewhat expanded	Very expanded
Suborbitals	Suborbitals	Maxillaries	Maxillaries	Maxillaries	Suborbitals	Maxillaries
Narrow	Somewhat wide	Wide	Expanded	Somewhat expanded	Wide	Very expanded
Low. Without short divergent crests in the parietal region	Somewhat projecting	Somewhat projecting	Projecting. Short divergent crests in the parietal region	Somewhat raised	Developed. No upper eyelid	Very well developed. An upper eyelid
Somewhat concave, granular. Without divergent crests at canthal apex	Somewhat concave and wide. Short divergent crests at canthal apex	Concave, wide, granular. Short divergent crests at canthal apex	Concave, very wide, granular. Short divergent crests at canthal apex	Somewhat concave, granular	Somewhat concave, deep, granular	Very concave, deep. Without granules
Not well marked	Scarcely visible	Poorly marked	Marked	Marked	Well marked	Well marked
Not expanded	Expanded laterally	Not well marked	Thick border	Well marked	Well developed	Very high
Gently sloping	Gently sloping	Gently sloping	Gently sloping	Gently sloping	Nearly vertical	Not well marked. Nearly vertical
Rather prominent. Dorsal granules rounded	Subtriangular, not well marked. Dorsal granules conical or flat	Thin, with poorly marked borders. Dorsal granules conical, horny	Not prominent. Dorsal granules flat	Not prominent. Dorsal granules smooth	Subtriangular. Lower border not well marked. Dorsal granules flat	Subtriangular. Lower border not well marked. Dorsal granules flat
Poorly marked	Not well marked	Present	Hardly noticeable	Not well marked	Absent	Absent
Present	Absent	Absent	Generally absent	Generally present	Present	Present



Map 2. Distribution of *Bufo granululosus* subspecies in northern South America.



Map 3. Distribution of *Bufo granulatus* subspecies in eastern Brasil.

Map 4. Distribution of *Bufo granulosus* subspecies in southern South America.